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LATE SUMMER–SPRING MOVEMENTS OF JUVENILE SAGE GROUSE

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ABSTRACT.—Late summer to early spring movements of radio-marked juvenile Sage Grouse (*Centrocercus urophasianus*) were studied on Cold Spring Mountain, northwestern Colorado, from July to February 1981–82 and August to May 1982–83. Movements were analyzed from 118 locations (N = 8 grouse) during July–November 1981 and 213 locations (N = 10 grouse) during August–November 1982. Grouse steadily moved away from capture sites until November each year when they moved to winter-use sites. Movements to wintering areas in late November were related to snowfall and subsequent availability of sagebrush. Maximum one-way distance to wintering areas was 30.3 km (N = 4 radio-marked grouse). Sage Grouse generally followed topographic features and avoided areas without sagebrush cover, although they were capable of long-distance (23 km) movements over areas without shrub cover. During spring recruitment there appeared to be roving groups of males, probably yearlings, that spent much of the breeding season displaying near females away from traditional leks. *Received 25 Feb. 1985, accepted 10 July 1985.*

Spacing behavior may produce changes in birth, death, and movement rates that subsequently limit population size (reviewed in Watson and Moss 1970, Krebs 1978). Red Grouse (*Lagopus lagopus scoticus*) are a classic example of the importance of summer and fall movements to recruitment into the breeding population (Moss et al. 1984). Although natal movements have been examined for Greater Prairie-Chickens (*Tympanuchus cupido pinnatus*) (Bowman and Robel 1977), Spruce Grouse (*Dendragapus canadensis*) (Keppie 1979), and Blue Grouse (*D. obscurus*) (Jamieson and Zwickel 1983a), movements of juvenile Sage Grouse (*Centrocercus urophasianus*) from summer ranges to breeding areas have not been studied. In this paper we present the first detailed report of the late-summer to early-spring movements of juvenile Sage Grouse.

STUDY AREA AND METHODS

The study was conducted on Cold Spring Mountain in northwestern Moffat County, Colorado, and in adjacent Wyoming and Utah from July 1981 through June 1983. The study area is semiarid sagebrush (*Artemisia* spp.) rangeland with interspersed quaking aspen (*Populus tremuloides*) and pinyon pine (*Pinus edulis*)-Utah juniper (*Juniperus osteosperma*) stands, and meadows. Lodgepole pine (*Pinus contorta*) and Douglas-fir (*Pseudotsuga menziesii*) occur above 2620 m on Middle Mountain (2904 m) and Diamond Peak (2909 m) on the northern edge of the study area. Cold Spring Mountain (2622 m) receives 46–51 cm

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of precipitation annually, of which 11% falls in August (U.S. Dept. Interior 1978). July-August trapping on Cold Spring Mountain yielded 120 to >300 banded juvenile Sage Grouse per year from 1978 through 1982.

Juvenile grouse were captured and individually marked with numbered aluminum bands and unique combinations of colored plastic bands in 1981 and 1982. Drive traps, a bumper-mounted cannon net, and spotlights and long-handled nets were used to capture grouse (Giesen et al. 1982). Captured birds were classified to sex and age by wing molt and length of primaries (Beck et al. 1975). Forty-two radio transmitters attached to poncho-type markers (Amstrup 1980) were placed on juvenile grouse during July and August 1981 and July through October 1982. Thirteen solar-powered radio transmitters were used in 1981, and 23 battery-powered and 6 solar-powered radio transmitters were used in 1982. Radio-marked birds were relocated at least three times weekly from 15 July to 31 August 1981 and from 1 August to 11 September 1982. Relocations were made at least monthly after 11 September to 15 November each year. During January to mid-April 1983, 4 radio-marked juveniles were relocated at least once a month. Weekly radio relocations were evenly divided into morning (≤4 h after sunrise), midday (>4 h after sunrise to >4 h before sunset), and evening (≤4 h before sunset) time periods. These time periods coincide with most feeding during morning and evenings, and roosting during midday. Radiolocations made on the ground were determined by triangulation at close range (approximately 200 m) or by flushing, and data were plotted on 7.5-min U.S. Geological Survey topographic maps. This was supplemented with radio-tracking from an aircraft on 3 November 1981 and 15 January 1983.

Distances moved by grouse from their capture sites were analyzed with 2-way analysis of variance (ANOVA) for interactions among individual birds and time periods. If the interaction was significant ($P < 0.05$), distance from capture site for each bird was regressed individually on other variables (age of bird, date, or movement rate). Directions were analyzed with nonparametric statistical tests (Batschelet 1978). Test results were considered significant at the 0.05 probability level.

RESULTS

Fifteen and 43 juvenile Sage Grouse were radiomarked in 1981 and 1982, respectively. Locations of only 8 birds in 1981 and 10 birds in 1982 were used for analysis because of radio signal losses, predation, hunter harvest, or incomplete data. Movements were analyzed from 118 locations in 1981 and 213 locations in 1982.

During both years grouse steadily moved away from their capture sites from August to November (Fig. 1). Because of unequal sample sizes and interaction effects (2-way ANOVA, $P = 0.01$) between individual birds and time periods, it was not possible to determine when increases in distances from capture sites occurred; however, the data indicate that increases were gradual during both years. Movement rates (km/day) did not vary with date in either year (Table 1). Distance from capture sites was highly correlated with date for 14 of 18 birds (Table 1). Three birds showed no relationship between distance from capture sites and date, age of bird, or movement rate. During 15 July to 4 September 1981 and 1 August to 4 September 1982, 84 and 78% of all locations (79/94 and 72/92, respectively) were ≤2 km from capture sites, while during 3 October

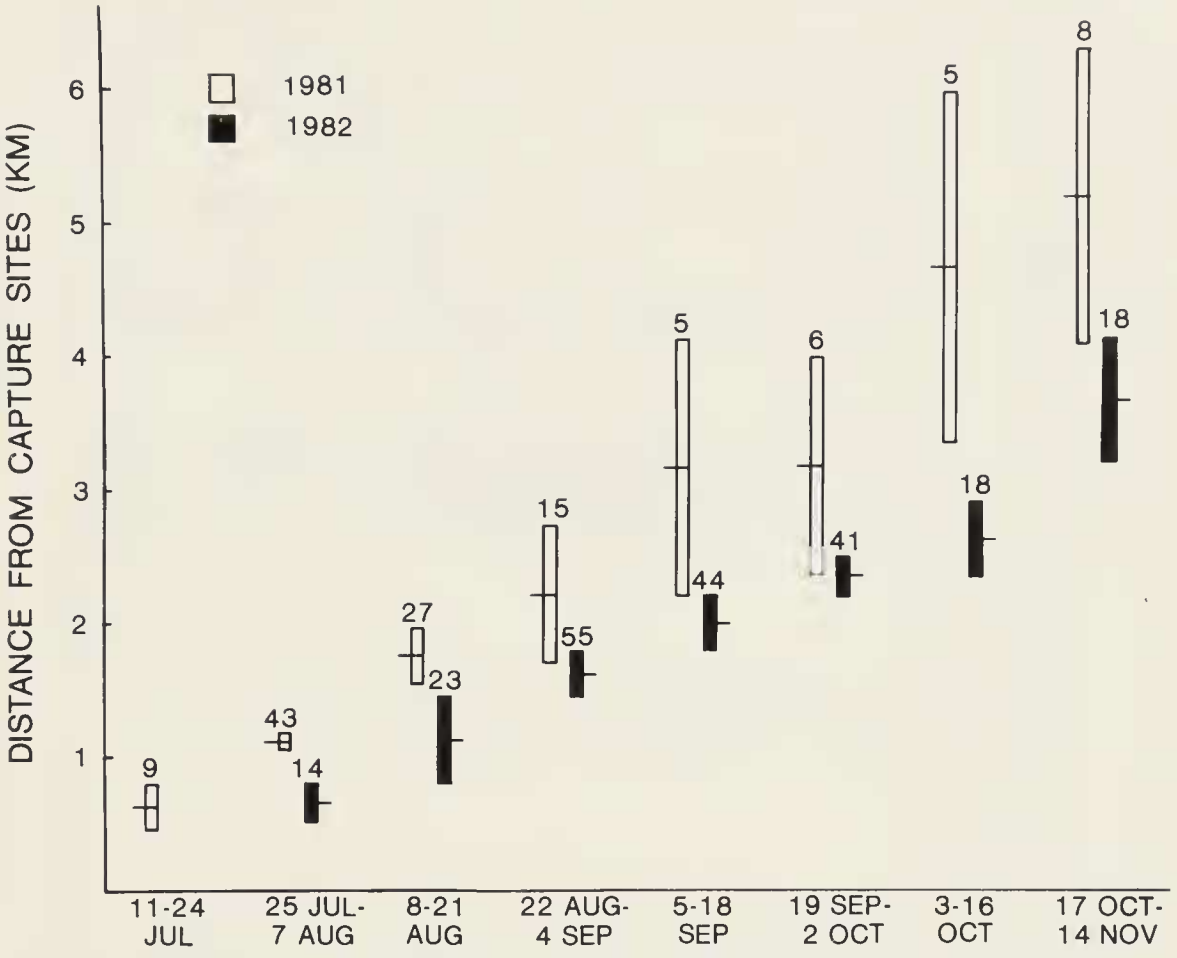

FIG. 1. Distance (km) moved from capture sites by 8 radio-marked Sage Grouse in 1981 and 10 grouse in 1982 on Cold Spring Mountain, Colorado. Horizontal line is the mean. The bar is one SE above and below the mean. The number above the bar is the number of radiolocations. Data are from 12 males and 6 females (Table 1).

to 14 November 1981 and 1982, 77 and 78%, respectively, of all radiolocations (10/13, 28/36) were >2 km from capture sites. In 1981, females were farther, on average, from their capture sites than males on any date after 10 August, while in 1982 males were farther, on average, from capture sites than females on any date after 1 August.

Movements of all but 3 (N = 18) birds in 1981 and 1982 had a nonrandom orientation, or significant mean direction, from capture sites (Rayleigh's test, $P < 0.00$) (Fig. 2). There was no significant mean direction when individual means of all birds were combined (Mardia's correlation coefficient, $P > 0.05$). Although we violated the test restriction that N should be equal for all birds, a slight variation of N has little effect on the statistical analysis (Batschelet 1978:6). Also, there was no obvious difference between directions of movements of males and females (Fig. 2). Males and females did not differ in mean direction moved in either year (Mardia-Watson-Wheeler test, $P > 0.05$).

Except for one male grouse (#501) found on Cold Spring Mountain on

TABLE 1

R^2 AND PROBABILITY (P)[a] OF SIMPLE AND MULTIPLE REGRESSION MODELS OF SAGE GROUSE DISTANCES FROM CAPTURE SITES (KM) WITH MOVEMENT RATE FROM PREVIOUS LOCATIONS (M/DAY), DATE, AND AGE OF BIRD ON COLD SPRING MOUNTAIN, COLORADO, 15 JULY–14 NOVEMBER 1981 AND 1 AUGUST–14 NOVEMBER 1982

Year	Bird	Sex	No. locations	Distance from capture sites, R^2 (P)				
				Movement rate	Date	Age	Best multiple model[b]	Variables in multiple model
1981	438	M	14	0.01 (>0.5)	0.22 (0.25)	0.22 (0.25)	None	None
	465	F	10	0.01 (>0.5)	0.77 (0.00)	0.77 (0.00)	0.77 (0.00)	Date or age
	486	M	16	0.01 (>0.5)	0.76 (0.00)	0.64 (0.00)	0.76 (0.00)	Date
	501	M	18	0.11 (0.30)	0.38 (0.01)	0.38 (0.01)	0.38 (0.01)	Date
	585	F	13	0.00 (>0.5)	0.66 (0.00)	0.66 (0.00)	0.66 (0.00)	Date
	687	M	11	0.00 (>0.5)	0.56 (0.01)	0.56 (0.01)	0.56 (0.01)	Date
	712	F	18	0.12 (0.4)	0.75 (0.00)	0.75 (0.00)	0.75 (0.00)	Date
	785	M	18	0.00 (>0.5)	0.57 (0.00)	0.57 (0.00)	0.57 (0.00)	Date
All birds			118				0.44 (0.00)	Date
1982	520	M	28	0.00 (>0.5)	0.59 (0.00)	0.60 (0.00)	0.60 (0.00)	Age
	562	F	18	0.48 (0.00)	0.10 (0.20)	0.08 (0.25)	0.69 (0.00)	Movement rate, age
	576	F	27	0.08 (0.15)	0.34 (0.00)	0.34 (0.00)	0.34 (0.00)	Date or age
	669	M	15	0.27 (0.04)	0.37 (0.02)	0.45 (0.00)	0.78 (0.00)	Age, movement rate
	694	M	21	0.06 (0.27)	0.00 (>0.5)	0.00 (>0.5)	None	None
	702	M	22	0.14 (0.09)	0.74 (0.00)	0.73 (0.00)	0.74 (0.00)	Date
	712	F	17	0.02 (>0.5)	0.67 (0.00)	0.67 (0.00)	0.67 (0.00)	Date or age
	734	M	15	0.04 (0.47)	0.56 (0.00)	0.56 (0.00)	0.56 (0.00)	Date or age
	757	M	28	0.02 (>0.5)	0.56 (0.00)	0.56 (0.00)	0.56 (0.00)	Date or age
	797	M	22	0.02 (>0.5)	0.10 (0.16)	0.09 (0.16)	None	None
All birds			213				0.59 (0.00)	Date, movement rate

[a] Probability of no relationship between distance from grouse capture sites and the independent variable.
[b] Stepwise multiple regression.

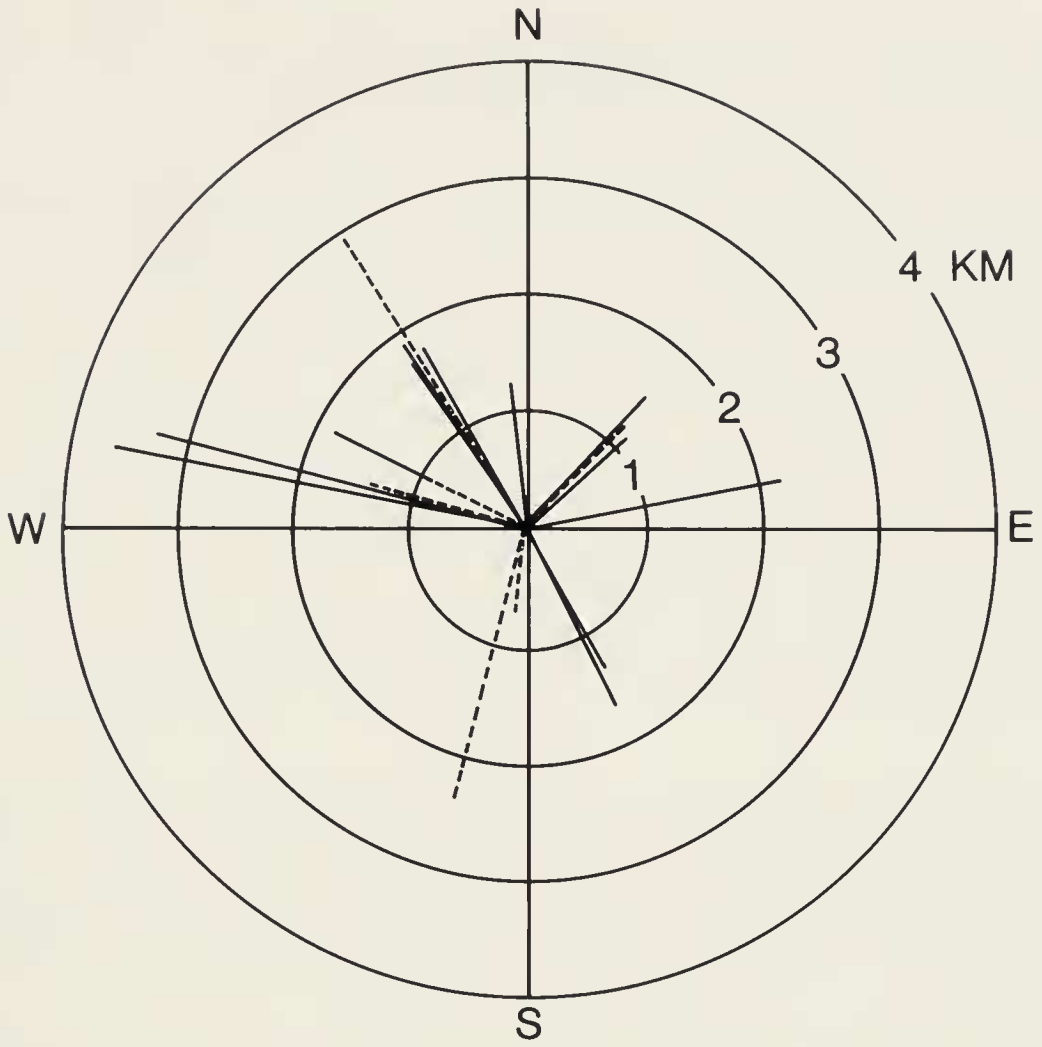

FIG. 2. Mean angles and mean distances (km) moved from capture sites of radio-marked juvenile Sage Grouse (N = 18) on Cold Spring Mountain, Colorado, July–November 1981 and August–November 1982. Solid lines are males (N = 12); dashed lines are females (N = 6).

21 January 1982, the last two radiolocations of juvenile grouse marked in 1981 were on 14 November. Male #501 and 35 other grouse were located in exposed sagebrush on 21 January 1982, but grouse were not seen after 2 Februray following a snowstorm that covered all exposed sagebrush. In fall 1982, 7 grouse were radiotracked until 14 November. One radio-marked adult hen was located on its wintering area 5 km northeast of Cold Spring Mountain on 15 December 1982. A juvenile male (#734, Fig. 3), which was radiotracked from August to November 1982 and January to May 1983, moved to its subsequent wintering area during 23–30 October 1982. The number of radio-marked grouse with known locations in 1982 decreased from 17 on 30 October to 7 on 14 November and to none on 25 November. During this period snow levels on Cold Spring Mountain increased from 0–5 to 20–50 cm. By 14

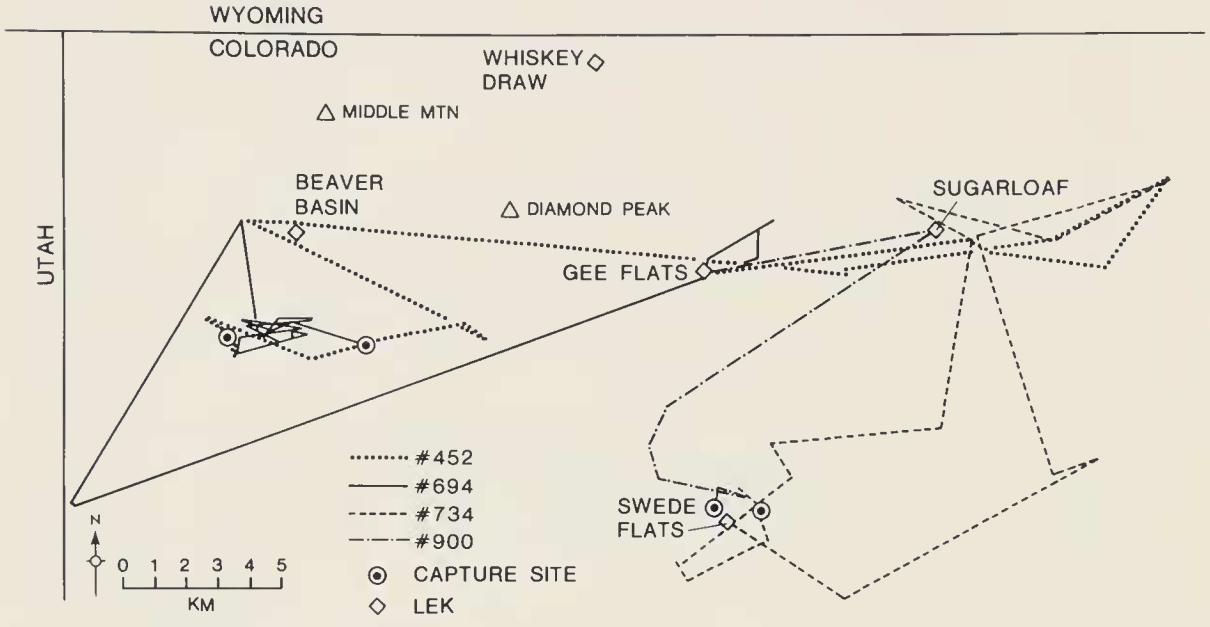

FIG. 3. Summer to spring movements of 4 radio-marked juvenile Sage Grouse (3 males; 1 female, #452) on Cold Spring Mountain, Colorado, 9 August–28 May 1982–83.

December, snow depth was ≥1 m and all sagebrush on Sage Grouse summer range was covered. Some birds appeared to leave summer range in late October–November, as 9 of the original 58 radio-marked grouse were lost prior to 3 October. None of these birds was later relocated, so we do not know if they were dispersing earlier than other grouse or whether there were other reasons for loss of radio signals. However, 4 of the 9 birds had moved ≥3 km when they were lost.

Four juveniles (3 males, 1 female) radiomarked in summer 1982 were located in January and February 1983 after being lost during late-November to mid-January. Maximum distance from capture sites to their locations in January–April 1983 averaged 18.2 km for these 4 birds. The female grouse moved a maximum of 30.3 km from her capture site, while the 3 males moved from 11.4 to 17.3 km from their capture sites (Fig. 3). Color-banded and radio-marked grouse were found wintering in two areas: one area was a 200-km^2 sagebrush flat 5–30 km northeast of Cold Spring Mountain; the other area (25 km^2) was 7 km southwest of Cold Spring Mountain along the Utah-Colorado boundary (Fig. 3). A radio-marked male (#694) in the latter wintering area moved 23 km to the wintering area northeast of Cold Spring Mountain between 2 February and 26 March 1983 and attended Gee Flats Lek, in the same area, from 4 April to 19 May (Fig. 3).

During the spring breeding season, all 4 radio-marked yearlings were observed on leks; however, male #734 appeared to spend most of the breeding season away from known leks. Male #734 and 6 other males were seen displaying near 3 females on the morning of 10 April, approx-

imately 2 km east of Sugarloaf Lek, and were again seen displaying on 14 April about 9 km southeast of Sugarloaf Lek. These areas were checked on six mornings, but no grouse were observed displaying regularly within 300 m of the initial locations. We did not observe male #734 on a known lek until late in the breeding season when it displayed on Swede Flats Lek on 25 May (Fig. 3). The 2 other radio-marked males spent totals of at least 22 and 9 days displaying on known leks. Female #452 was located approximately 1 km southeast of Sugarloaf Lek on four mornings during 3–10 April and on Gee Flats Lek on six mornings during 21–27 April. On mornings when female #452 was located with other females 1 km southeast of Sugarloaf Lek, groups of 5–6 males displayed nearby and followed the females through the sagebrush; the locations of these males were not considered leks because they moved daily. These observations suggest that there are roving groups of males, probably yearlings, that spend much of the breeding season displaying near females away from traditional lek sites.

DISCUSSION

Late summer movements of juvenile Sage Grouse on Cold Spring Mountain were not characterized by rapid, synchronized movements by most members of the population, as Godfrey and Marshall (1969) found for Ruffed Grouse (*Bonasa umbellus*). Instead, movements of both sexes on Cold Spring Mountain were sporadic throughout September and October, similar to those reported for Greater Prairie-Chickens (Bowman and Robel 1977) and Sage Grouse in Idaho (Dalke et al. 1963). Movement rates on Cold Spring Mountain did not change during September–November because movements of >2 km were quick (about 1 day) and separated by periods of up to 20 days when birds did not move >0.3 km/day. We were unable to determine if there was a difference in movements between male and female Sage Grouse; however, no difference between the sexes was suggested by the longer movements of females than males in 1981 and the reverse in 1982.

Sage Grouse tended to follow topographic features and avoided areas without sagebrush cover, as mean angles of summer movements were generally along the northwest to southeast orientation of Cold Spring Mountain and away from its steep (80% slope) southwest face which was covered with pinyon-juniper forest. Sage Grouse, however, may cross large areas without cover as did radio-marked male #694, which crossed Cold Spring Mountain when all sagebrush on the mountain was snow covered.

Synchronized, long-distance movements to winter range may have occurred during mid-November to mid-January as locations of most radio-

marked birds were unknown during that time. Field observations indicated that Sage Grouse generally moved north to sagebrush flats and lower valleys as snow levels increased in November. Patterson (1952), Dalke et al. (1960), and Schoenberg (1982) reported that Sage Grouse movements between wintering and breeding (leks and nesting sites) areas were related to snow level and its effect on the availability of sagebrush. Movement distances probably varied depending on the distance to suitable cover above snow. Patterson (1952) and Dalke et al. (1960) reported one-way movements from summer to winter ranges of up to 160 km in Wyoming and Idaho, respectively. In Colorado, winter to breeding range distances averaged 28–30 km for 7 radio-marked grouse (4 females, 3 males) (Schoenberg 1982) and 8–12 km for color-banded grouse (68 males, 10 females) traveling from breeding to winter ranges (Beck 1977).

Another study of fall movements of radio-marked Sage Grouse (both adults and juveniles were tracked until 30 November) found that grouse generally left summer range in October and November (Connelly and Markham 1983). From 10 July to 7 September, 95% of all radiolocations (N = 131) in the Idaho study were ≤ 2 km from the general capture area, while 82% of all locations (N = 22) were >2 km during October to November. These findings are consistent with results from Cold Spring Mountain. Three of 14 radio-marked grouse in Connelly and Markham's (1983) study moved from summer range prior to mid-September, while most birds did not leave until after 1 October.

During summer 1982, one yearling female and at least 2 chicks may have exhibited posthatching emigration as described by Watson and Moss (1980). From hatching during 25–27 June until 7 August, the hen and chicks were ≤ 2.5 km from the nest site. On 7 August the female and chicks (45–47 days old) were 5.2 km from the nest site; the next day they were 9.6 km from the nest. The female was last seen with a chick on 17 August and had started moving back towards the nest site on 12 September. The hen was last located 2.2 km from the nest site on 3 October. In contrast, one other radio-marked female with a brood remained within 2 km of her nest site until loss of the radio transmitter on 8 August, and one of her chicks, which was radio-marked, did not move >2.1 km from the nest site until 12 September. Among 7 radio-marked females which were unsuccessful nesters, maximum distance from nests averaged 3.8 km prior to 20 August (range 1.3–6.5 km). Early dispersal or posthatching emigration may increase a yearling's chances of recruitment if there is a lower probability of establishing a territory in natal than in other areas.

During spring recruitment in lek species, it appears that some yearling males may only display infrequently on leks, or not at all. Robel (1969, 1970) observed radio-marked yearling Black Grouse (*Lyrurus tetrix*) and

Greater Prairie-Chickens that rarely attended leks, and Lill (1974) has described male White-bearded Manakins (*Manacus manacus*) engaged in courtship behavior away from leks. Similar evidence for a subpopulation that does not attend leks comes from a removal experiment with Sharp-tailed Grouse (*Tympanuchus phasianellus*) in which grouse recruited onto removal leks were probably nonterritorial yearlings (Rippin and Boag 1974). It may be advantageous for yearlings to postpone territory establishment on a lek until later years if territories which might lead to high mating success cannot be acquired easily during their first spring, as has been suggested for Blue Grouse (Lewis and Zwickel 1982, Jamieson and Zwickel 1983b).

ACKNOWLEDGMENTS

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ERRATA

In "A list of birds and their weights from Saul, French Guiana" by James A. Dick, W. Bruce McGillivray, and David J. Brooks (Wilson Bull. 96:347–365, 1984); paragraph 7 on page 355 should be deleted, as the wet specimen identified as a Tiny Tyrant-Manakin was determined to be a White-fronted Manakin (*Pipra serena*). On page 358, Bicolored Conebill . . . should read "White-shouldered Tanager (*Tachyphonus luctuosus*).—A wet specimen in juvenal plumage (KU 73387) 12 g, 17 February 1977, subsequently identified by Dr. K. C. Parkes." On page 359, under the heading "Conclusions and Summary" the last two lines of the first paragraph should read "Two species were reported in French Guiana for the first time. They were: *Neochelidon tibialis* and *Vireo altiloquus*." On page 363 under the heading "Appendix," line 21 should be deleted. On page 364, *Conirostrum bicolor* should read "*Tachyphonus luctuosus*."